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MENDELIAN PROPORTIONS AND THE INCREASE OF RECESSIVES

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RECENTLY in working over some data[1] on the inheritance of lefthandedness, certain questions came up, which seem of considerable interest, as: Does the proportion of lefthanded people remain the same from century to century or does it diminish or increase? In any case, how does the result come about? Although well aware of the present-day aversion to arm-chair biology, it yet seems that these problems can hardly be attacked from the experimental side, and that a theoretical discussion may be of some value.

It may be stated at the outset that I consider lefthandedness to be a true Mendelian recessive,[2] and also that there is no selective mating with reference to the character. There seems also no reason to suspect that lefthanded people exhibit less fertility[3] than normal individuals. If these suppositions are correct, the condition offers a happy opportunity for study, since most human characters thus far examined are such as might be likely to be affected by selection.

Concerning the first question asked above, no positive answer can be given, for there are no statistics. It is probable that the affection is a very old one, and not of recent origin. If it tends to increase it might be expected that a very considerable part of the population would now show the condition, while if it is decreasing, we should, after all the long period of its existence, find only a few persons with the condition.

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[1] As yet unpublished.

[2] Evidence for this view is shown by Professor H. E. Jordan in the *Breeders' Magazine*, Vol. II, pp. 19–29 and 113–124. My own observations confirm this belief.

[3] My own records even suggest the opposite condition, but this is probably merely chance due to the small numbers studied.

On the "presence and absence" theory lefthandedness is due to the loss or "dropping out" of the factor or determiner for righthandedness. If such loss could occur in the past, why not from time to time now? If so, why would not the proportion of lefthanded people continually increase?

In a population where the dominant, the heterozygote and the recessive have a certain proportion, slight changes in the relative numbers seem to have no permanent effect. There is a tendency to stability and unless a certain point is passed because of the appearance of an unusual number of recessives, there will be a return to the usual ratio. The mathematical features of the case have been discussed by Dr. W. J. Spillman,[4] and by Mr. G. H. Hardy.[5] The earliest clear statement of the case which I have seen is by Dr. George H. Shull[6] in his discussion of elementary species in *Bursa bursa-pastoris.*

The fact of the stability of certain ratios and instability of others can be readily comprehended from the following tables (I, II, III). We may let RR represent a pure righthanded individual, Rr, a heterozygous righthanded individual, and rr, a lefthanded individual. As a first example it may be supposed that a large population exists in which the various types occur in the following proportions, viz.:

1 pure righthanded : 2 heterozygous righthanded :
1 lefthanded, or,

$$RR : 2Rr : rr.$$

Random matings would occur in such fashion that members of each group would mate with those of their own group or with members of other groups. The various possibilities are represented in Table I. The filial generation derived in Table I is composed of the three types in the same ratio as in the parental generation.[7]

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[4] *Science,* N. S., Vol. XXVIII, pp. 252–254, 1908.

[5] *Ibid.,* pp. 49, 50.

[6] *Science,* N. S., Vol. XXV, pp. 590, 591, 1907.

TABLE I

MATINGS AND OFFSPRING IN A LARGE POPULATION HAVING THE COMPOSITION 1 RIGHTHANDED: 2 HETEROZYGOUS RIGHTHANDED: 1 LEFTHANDED ($RR : 2Rr : rr$)

Matings	Offspring		
	RR	Rr	rr
$RR \times RR$	1		
$RR \times 2Rr$	1	1	
$RR \times rr$		1	
$2Rr \times RR$	1	1	
$2Rr \times 2Rr$	1	2	1
$2Rr \times rr$		1	1
$rr \times RR$		1	
$rr \times 2Rr$		1	1
$rr \times rr$			1
Totals	4	8	4
or	1	2	1

As a second example, the ratio 2:2:2 may be taken. This will give the results shown in Table II. The ratio 2:2:2 is not constant, but stability is reached in F_1, which is found to show the same ratio as our previous case, viz., 1:2:1.

TABLE II

MATINGS AND OFFSPRING IN A LARGE POPULATION HAVING THE PROPORTION 2 RIGHTHANDED: 2 HETEROZYGOUS RIGHTHANDED: 2 LEFTHANDED ($2RR : 2Rr : 2rr$)

Matings	Offspring		
	RR	Rr	rr
$2RR \times 2RR$	4		
$2RR \times 2Rr$	2	2	
$2RR \times 2rr$		4	
$2Rr \times 2RR$	2	2	
$2Rr \times 2Rr$	1	2	1
$2Rr \times 2rr$		2	2
$2rr \times 2RR$		4	
$2rr \times 2Rr$		2	2
$2rr \times 2rr$			4
Totals	9	18	9
or	1	2	1

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[7] I am indebted to my colleague, Professor Saul Epsteen, of the Department of Mathematics, for checking my method of analysis.

In Table III a few possible matings are shown with the percentage of recessives and the constant ratios which appear in the next generation. It is apparent from examination of the figures that if a disturbance takes place there is often a partial return in the next generation to the original condition. Sometimes this return is complete, as would occur if, beginning with the ratio of 1:2:1, some disturbance should make it 1:1:1. In the next generation there would be a return to the 1:2:1 condition. There were 25 per cent. of recessives at the beginning. This became changed to 33.3 per cent. by mutation but returned in the next generation to 25 per cent.

TABLE III

EXAMPLES OF RATIOS OF DOMINANTS, HETEROZYGOTES AND RECESSIVES, TOGETHER WITH THE CONSTANT RATIOS DERIVED IN THE FIRST FILIAL GENERATION. THE CONSTANT RATIOS ALL HAVE THE FORM $A^2 + 2AB + B^2$

Original Ratio	Per Cent. Recessives	Constant Ratio in F_1	Per Cent. Recessives
1 : 1 : 1	33.3	1 : 2 : 1	25.0
1 : 1 : 2	50.0	9 : 30 : 25	39.0
1 : 1 : 4	66.6	1 : 6 : 9	56.2
1 : 2 : 1	25.0	Constant	Constant
1 : 3 : 1	20.0	1 : 2 : 1	25.0
1 : 3 : 2	33.3	25 : 70 : 49	34.0
1 : 4 : 4	44.4	Constant	Constant
2 : 1 : 2	40.0	1 : 2 : 1	25.0
4 : 4 : 1	11.1	Constant	Constant
4 : 6 : 1	9.0	49 : 56 : 16	13.2

But there is not always a diminution of this kind. If the original ratio be 4:4:1, which is constant, and this be changed by mutation to 4:6:1, the original 11.1 per cent. of recessives is at first reduced to 9 per cent., only to rise in succeeding generations to 13.2 per cent. It is very easy to overestimate the importance of the tendency to return to a stable ratio, since such stable ratios are practically without limit, and instead of returning to the same ratios, it is easily possible to reach stability in a new ratio somewhat different from the original. This may be shown by an example (Table IV).

TABLE IV

Figures Showing the Formation of a New Stable Ratio in a Population having at First the Composition 4 : 4 : 1 when a Small Number of Heterozygotes become Recessives through Mutation

Ratio in the original population: 400 : 400 : 100 = 11.1 per cent. recessive.
Ratio after mutation: 400 : 396 : 104 = 11.5 per cent. recessive.
Ratio of the next generation: 89,401 : 90,298 : 22,801 = 11.2 per cent. recessive.

The change in any case is not so simple as mathematical study would at first suggest, for many of the individuals mate with members of earlier or later generations. When a considerable number of recessive mutants appear in a given generation this excess is, in part, reduced by matings with members of the normal generations before and after them. Hence a return to the normal or usual condition is made easy. These considerations naturally suggest a reason for the comparative stability of species within a genus or of elementary species within a Linnæan species.

From what has been said it will be seen that unless a recessive character is arising by mutation at some appreciable rate there will be little or no increase in the proportion of individuals exhibiting this character. On the other hand, whenever a considerable number of mutants do appear the normal condition of equilibrium is disturbed and a new stable ratio becomes established in which the recessives are in larger proportion.

There are probably many recessive characters which are not the objects of natural selection by the environment nor of sexual selection in mating. Lefthandedness may well be such a character. It certainly seems that the proportion of individuals with such characters will increase slowly through long periods of time. Let it be supposed, for example, that the proportion of dominants, heterozygotes and recessives in the general population is 9:6:1. Now it is probably far easier in mutation for a given factor to drop out than to be added. If, however, the dropping out and addition could take place with equal facility, there would still be much in favor of the recessive. In the supposed ratio 9:6:1 it is possible for any one of the dominants or heterozygotes to lose a determiner. In other words, on the average fifteen out of sixteen individuals have an opportunity to vary toward lefthandedness; that is, 93.9 per cent. On the other hand, only the heterozygotes and the recessive can vary toward righthandedness; seven out of sixteen, therefore, have this possibility, or 43.7 per cent. of the population. If, therefore, the addition of the factor were as easily accomplished as the loss of the factor—which is probably never true—loss of a factor would be more than twice as likely to occur as gain. With the ratio 1:2:1 opportunities are of course equal for upward and downward mutation. In a population with more than 25 per cent. of recessives, the number of heterozygotes plus recessives is greater than the number of heterozygotes plus dominants, as, for example, with the ratio 1:4:4, in which the recessives make up 44.4 per cent. of the population.

It would seem from the above that there is a constant tendency for the proportion of individuals showing nonimportant recessive characters to increase, unless indeed mutative changes occur so slowly that the population is constantly held back to a stable ratio. We are led naturally to the thought that for species in general the individuals showing recessive mutations may be expected to increase at the expense of the original type, unless the characters lost are of some real importance to existence or to mating. Just this sort of thing has probably taken place with the shepherd's purse, *Bursa bursa-pastoris*. It can hardly be doubted that the numerous species described by Almquist[8] are derived from a single original species. If the total number of *Bursas* in the world remains the same from century to century and these elementary species appear in some number from time to time, they must be crowding upon the original form. Other examples in great number will occur to any one. Thus there can be little doubt that primitive man was dark-skinned and dark-eyed. The various modern races were produced—so far as skin-color and eye-color are concerned—by dropping out the factors (determiners) for these characters. In our own Caucasian race, it seems not unreasonable to suppose that we are tending toward a condition of blondness, for there seems to be no natural or sexual selection against this character.[9]

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[8] Noted by Dr. George Harrison Shull, "Advance Print from the Proceedings of the Seventh International Zoological Congress, Boston Meeting, 1907."

I am not unmindful of the fact that an apparently unimportant character such as righthandedness may be bound up with other characters of great consequence. In such case lefthandedness might mean, for example, a distinct inferiority in metabolic activity.[10] Unless the recessiveness is associated with weakened nutrition or other enfeebled condition, it would seem most natural for elementary species, when once originated, to increase in number of individuals by continued mutation.

Dr. Shull points out in his paper previously cited on "Elementary Species and Hybrids of *Bursa*" that recessive mutants may have an advantage over dominant mutants if fluctuating conditions tend to eliminate now one form, now the other. The killing off of dominant mutants may be easily accomplished, but this is not the case with recessives.[11] This is perhaps only another way of stating the well-known fact that it is hard in plant or animal breeding to get rid of recessive characters which are not wanted.

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[9] The claim that light-skinned and light-eyed people are not adapted to sunny climates seems hardly substantiated.

[10] Cf. the observations by Professor Thomas Hunt Morgan upon mutants of the fruit fly, *Drosophila*, in the *Journal of Experimental Zoology*, Vol. XI, p. 408, 1911.

[11] To use his own words: "The recessive mutant may be preserved indefinitely under the protection of the dominant characteristics of its more successful parent. Such prolongation of the life of a recessive may serve to tide it over times of special stress or may continue its existence until the various distributing agents have carried it beyond the limits of the habitat in which it is a failure into others in which it may become a success." This same idea has been suggested by my colleague, Professor T. D. A. Cockerell, in a conversation regarding the general question of increase of recessives.

SUMMARY

In the foregoing discussion an attempt has been made to exhibit clearly the facts of stable ratios involving Mendelian dominants, heterozygotes and recessives. While suggested by a study of lefthandedness, what has been said will apply to any recessive character which is not selected against in mating and which does not affect the success of the organism in other ways. I have tried to accord full value to the mathematical features of the case, and have pointed out the various checks which tend to hold the population in a given ratio. Yet I have been unable to escape the conclusion that recessive mutants, unless inherently weak in some respect, must tend to increase in numbers at the expense of original dominant types. These conclusions are reached from a consideration of the following points: (1) The greater ease with which characters may be lost than gained. (2) The great number of combined dominants and heterozygotes which through mutation may reach a simpler condition as compared with the small number of recessives and heterozygotes which may be imagined as affording opportunity for mutation to dominance.[12] (3) The more likely survival of recessives in an environment of changing conditions in which now the dominant and now the recessive is hard pressed to maintain its existence.

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[12] Unless the ratio of the three types is 1 : 2 : 1, when the opportunities are the same in each direction.